

Behavioral Responses of Female Oriental Fruit Flies to the Odor of Papayas at Three Ripeness Stages in a Laboratory Flight Tunnel (Diptera: Tephritidae)

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Behavioral responses of adult female oriental fruit flies, Dacus dorsalis Hendel, to the odor of papayas from three ripeness classes were studied using a three-choice flight tunnel bioassay. Laboratory-reared flies were allowed to respond freely to any of three papaya odors (mature green, color-break to one-fourth ripe, and one-half to full ripe) emanating from identical (spherical) fruit models. Five behaviors were measured in assessing the fly's relative attraction to the odors (number of landings), arrestment (total fly seconds on sphere), fly-fly interactions on the fruit model (maximum and modal fly density), and acceptance for oviposition (total eggs laid). Females showed no significant difference in total fly landings based on all age classes combined. Significant differences were noted among age classes. Females spent more total time on the sphere and showed a higher maximum density and modal fly density to ripe fruit than to green fruit odors. Ovipositional acceptance of fruit models based on the total number of eggs laid in a sphere was greater in response to the ripe-fruit odor than to the other two odor classes. Olfactory-stimulated behavioral responses of females to the odor of ripe papayas were significantly different from the other ripeness classes for all behaviors at 8 days postemergence and then declined in 11-day-old flies. Behavioral responses were greater during the afternoon than in the morning. Observations of wild oriental fruit flies to papayas in the field indicated a preference for residing on riper fruit. The results of this study are discussed with regard to the role of olfactory inputs generated by the odor

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of ripening fruit on female attraction and oviposition behavior resulting in infestation of papayas by oriental fruit fly.

KEY WORDS: Insecta; behavior; olfaction; oviposition; *Dacus*; preference; infestation.

INTRODUCTION

The oriental fruit fly, *Dacus dorsalis* Hendel, is a major quarantine insect pest in Hawaii and is considered to be the primary quarantine insect pest of commercially grown papayas, *Carica papaya* L. (Seo *et al.*, 1982; Couey *et al.*, 1984; Liquido *et al.*, 1989). Infestation of papayas by oriental fruit fly has been reported to be highly correlated with fruit ripeness (Seo *et al.*, 1982; Liquido *et al.*, 1989) based on field collection of fruits found to be infested and subsequent ripeness determination based on fruit skin color (Liquido and Cunningham, 1990). Although these studies pointed out the importance of fruit ripeness (based on color) in host infestation, they did not study female behaviors or interactions leading up to oviposition. Little is known about how semiochemical odors associated with ripening papaya might influence behavior(s) associated with host selection and oviposition in oriental fruit flies. Chemoreception is thought to play a major role in host-plant finding and oviposition in phytophagous diptera (Schoonhoven, 1982). It may also be important in either deterrence or a fly's acceptance of a host substrate. High levels of the chemical benzylisothiocyanate (BITC) in green papaya tissue was correlated to the relative lack of infestation and survival by oriental fruit larvae in green papayas (Seo *et al.*, 1983). Recently Flath *et al.* (1990) identified the volatile constituents of intact papayas at several different ripeness stages. Electroantennogram responses of both male and female oriental fruit flies to most of these compounds have been recorded (E.B.J. and D.M.L., unpublished data). In this study we investigated the influence of ripening papaya odors on attractancy and oviposition behavior of oriental fruit fly females in a laboratory wind tunnel (flight tunnel) assay. Our objectives were (1) to demonstrate a role for olfaction in host selection by oriental fruit flies, (2) to determine preference of female flies for odors from papayas of three ripeness classes using behavioral assays, (3) to assess the effects of fly age and time of day on quantifiable behavioral events in the wind tunnel, and (4) to compare our results with field observations of oriental fruit fly distribution and host infestation.

MATERIALS AND METHODS

Papaya (*Carica papaya* L. cv. Kapoho Solo) fruit were collected after harvest from a commercial papaya packing house on the island of Hawaii. Fruit were chosen based on their visual ripeness appearance and size and were free

from obvious defects, infestation, or disease. Each fruit was washed to remove dirt and fungicide and allowed to dry. Color readings of the blossom end and most yellow spot were then obtained for each fruit using a Hunterlab Labscan Spectrocolorimeter (LS5100, Hunter Associates, Reston, Va.) as reported by Flath *et al.* (1990) and Liquido and Cunningham (1990). The Hunter b value readings, a measure of the color of the fruit surface using a blue-to-yellow color scale, were recorded for both the blossom end and the most yellow spot on the fruit. In order to allow sufficient spatial separation of odor sources in the wind tunnel for behavioral bioassays, we categorized and used fruit of three general ripeness classes rather than the four classes reported by Flath *et al.* (1990). Mature green fruit were those that had no apparent yellow color on the fruit. Color-break to one-fourth-ripe fruit were those that showed some yellow color, usually found on the blossom end. Fully ripe fruit had a uniform yellow color. The range of b value readings for all fruit in each ripeness category, the mean b value, and the combined average weight of the two papayas used in each ripeness class for the bioassays are shown in Table I.

Laboratory-reared oriental fruit fly pupae were obtained from the USDA-ARS Tropical Fruit and Vegetable Research Laboratory's mass rearing facility in Honolulu, Hawaii. Flies of both sexes were allowed to emerge in 30 × 30 × 30-cm screened cages containing sugar, hydrolyzed protein, and water at 24–26°C, 60–70% RH, and 12/12 L/D cycle. After a minimum period of 6 days postemergence, cages were placed in a cold room where females were segregated from males and placed into lots of 50 females in plastic containers (11.5 cm in diameter, 7.5 cm deep) with nylon mesh covers and containing sugar, hydrolyzed protein, and water. Flies used in the bioassays were held at least 24 h at room temperature (24°C) after sexing. Flies from eight age classes

Table I. Hunter b Value Colorimeter Readings Used to Determine Ripeness and Combined Weight of Papayas Used in Flight Tunnel Assays

	Combined wt. ^a	Hunter b value	
		Blossom end	Most yellow spot
Mature green			
Range	690–840	12.2–16.6	10.7–20.6
$X \pm SD$	750 ± 51	14.4 ± 2.1	14.9 ± 4.7
Color-break-1/4 ripe			
Range	700–975	15.2–24.1	13.9–30.3
$X \pm SD$	793 ± 74	18.6 ± 3.7	20.8 ± 6.7
Ripe			
Range	700–905	23.8–36.3	28.8–37.3
$X \pm SD$	800 ± 74	30.1 ± 3.5	27.5 ± 14.7

^aWeight of two papayas which were used as a source of odor.

(6, 8, 9, 10, 11, 15, 16, and 19 days postemergence) were tested to evaluate the effects of age on observed behaviors. All age classes were combined for initial data analysis as noted in the text.

A rectangular flight tunnel (wind tunnel) ($261 \times 85.5 \times 86.5$ cm), constructed from tempered glass on all sides and having inlet and exit variable-speed box fans attached to galvanized sheet metal enclosures, was used as the bioassay arena. A laminar airflow system was established in the flight tunnel through the use of diagonally placed aluminum screen mesh and a honeycomb of horizontally stacked plastic drinking straws placed in front of the fan on the inlet side of the tunnel. A laminar flow of 20 cm/s was used for all studies in the wind tunnel, primarily using the inlet fan to "push" air through the tunnel. The tunnel was evenly illuminated by 40-W fluorescent lights (25–35 footcandles) at a room temperature of 24–26°C and 60–70% RH.

Initial dual-choice tests using only ripe papaya odor versus an air-alone control were run to establish whether there were differential responses in fruit fly attraction, arrestment, and ovipositional behaviors to the papaya odors. Subsequently a three-choice assay using the odors from each of three ripeness classes of papayas were run to determine the influence of olfaction on host-fruit selection by oriental fruit fly females. Two additional observations (maximum density and modal density) were included in the analysis of the three-choice assays as a means of assessing fly–fly interactions which might occur on the fruit.

Two papayas of a particular ripeness class (Table I) were placed in one of three sealed, all-glass containers containing inlet and exit ports on the top of the container. Breathing-quality compressed air from a tank was flushed over the papayas through 0.25-in. Teflon tubing attached from the tank to a three-way splitter which routed equal airflows to the inlet port of each of the three glass containers and exiting at the bottom of each container. Headspace odors from the papayas of each ripeness class were flushed through the outlet port of their own container via 0.25-in. tubing, then reduced to 0.125-in. Teflon tubing prior to entering the flight tunnel. The 0.25-in. tubing was connected to one of three perforated 7.5-cm round hollow polyethylene spheres (McInnis, 1989) which allowed odors to enter and emanate through holes in the sphere. The flow rate into each sphere was maintained at 50 cm³/min for each of the tests. The three yellow spheres [each emanating the odors from two papayas of a given ripeness class (Table I)] were hung in a row equidistant from one another and from the sides of the flight tunnel (16 cm) and 34 cm from the top of the tunnel.

For each assay, 50 flies were released from a platform at the downwind end of the tunnel and allowed to move freely within the tunnel for 30 min. During the course of the assay data on the number of flies landing on each of the odor emanating spheres and the duration of time spent on the spheres were recorded. Each sphere was monitored for the number of flies landing irrespective of whether or not they had previously visited the same or adjacent spheres.

Total (fly) time on the sphere was recorded by activating a digital timer upon the landing of the first fly and times of subsequent fly landings noted. When a fly left the sphere, the cumulative time of the most recent fly to visit the sphere was noted even if it was not the same fly which had just departed. Cumulative fly-seconds were then added at the end of the assays to determine the total time of flies on the sphere. This method was used due to the large numbers of flies which were frequently seen to flit on and off the spheres, which made tracking of individual flies on each sphere difficult. The method used to record total time on the sphere allowed us also to quantify the maximum density of flies on a given sphere during the course of the assay ("maximum fly density"), as well as the density of flies which was most frequently present on a sphere ("modal fly density") over the course of the 30-min assay. At the conclusion of the assay, flies were removed from the tunnel and the total number of eggs laid by all flies in a sphere determined by gently rinsing the inside of the sphere with water to remove the accumulated eggs. Data were analyzed on PC SAS Version 6.03 using PROCGLM on an Everex Model 1800 PC. Significant differences between the means were determined using ANOVA and Duncan's multiple-range test at the $\alpha = 0.05$ level. Dual-choice means were compared using a paired *t* test.

Field Observations

The distribution of oriental fruit flies on fruit of different ripeness classes were counted from 30 trees in a papaya orchard which was not being regularly harvested. The field was located in a papaya growing area near Hilo, Hawaii. Ten adjacent trees, located in three randomly picked rows and containing fruit of all ripeness classes, were observed during a 1-h period (12 noon–1 PM). For each tree two observations were made: (1) the numerical distribution of fruit of each of ripeness class (green, mature green, color-break, ripe, and overripe) based on visual appearance and (2) the number of flies observed on the fruit of various ripeness classes. The data were combined for all 30 trees and differences in numbers between ripeness classes of papayas, the number of flies per ripeness class, and the total number of flies per tree of each ripeness class were compared using *t* tests.

RESULTS

Initial tests in the flight tunnel to assess the ability of female oriental fruit flies to discriminate between the odor of ripe papayas and an air control showed clear preference for ripe papaya odor based on the number of fly landings, cumulative time spent on the spheres, and number of eggs deposited (Table II). A greater degree of each of the noted behaviors was elicited by the ripe papaya

Table II. Responses of Female Oriental Fruit Flies to Odors from Intact Ripe Papayas or Air Alone Emanating from Yellow Polyethylene Spheres in a Laboratory Flight Tunnel^a

Behavioral assay	Papaya odors	Air (control)
Total time on sphere (s)	6887 ± 1149**	825 ± 106
Total fly landings	5.6 ± 0.68*	1.6 ± 0.40
Total number of eggs laid	167 ± 46**	0

^aFifty laboratory-reared mated females (12 days old) were allowed to respond freely to odors emanating from 7.5 cm hollow polyethylene spheres (McInnis, 1989) during a 30-min bioassay. Values represent the mean ± SE responses from five replicates.

* $P < 0.05$ (paired t test).

** $P < 0.01$ (paired t test).

odor than by the control ($P < 0.05$). The number of eggs laid in the sphere was particularly indicative of strong olfactory discrimination and preference, in that no eggs were laid in the spheres emitting air alone while the number of eggs laid by females in the sphere emitting ripe papaya odor averaged 167 eggs/assay. The average number of eggs per female landing (total number of eggs laid per total number of females landing) ranged from 8.3 to 43.3 eggs/female over the five replications.

Females (all ages combined) given the opportunity to choose among the odors from three ripeness classes of papayas landed about equally on the three choices (Table III). However, the total cumulative seconds spent on a sphere by flies was significantly different between ripe papaya odor and mature green papaya odor. Comparisons between green papaya odor and color-break to one-fourth-ripe papaya odors, and color-break to one-fourth-ripe and ripe fruit odors were not significantly different. The total eggs laid in spheres emitting ripe papaya odor were greater than the egg counts for the other two ripeness classes. The total eggs laid in the three choice tests were less than the the totals for the dual-choice assays. This may be due in part to the fact that the flies were having to make a finer discrimination between spatially closer spheres in the three-choice assays than in the dual-choice assays. More importantly, in the three-choice assays, females were discriminating among three different odors rather than merely between the presence and the absence of fruit odor as in the dual-choice tests. The maximum fly density was greater on the sphere emitting ripe papaya odor than on the sphere emitting mature green papaya odor, but was not significantly different from color-break-one-fourth-ripe papaya odor (Table III). The modal fly density, the density of flies which were most often present on the sphere, was significantly higher on the ripe papaya odor sphere than on

Table III. Responses of Female Oriental Fruit Flies to Papaya Odors of Three Ripeness Classes in a Laboratory Flight Tunnel

Behavioral response ^a	Fruit odor category		
	Ripe	CB-1/4 ripe	Mature green
Total fly landings	8.9 ± 0.85a*	7.9 ± 0.90a	6.7 ± 0.80a
Max. fly density ^b	4.7 ± 0.47a	3.7 ± 0.36ab	3.3 ± 0.33b
Modal fly density ^c	2.9 ± 0.33a	2.2 ± 0.24ab	1.8 ± 0.18b
Total fly seconds ^d	3814 ± 501a	2925 ± 378ab	2312 ± 282b
Total eggs laid	21.1 ± 4.9a	6.4 ± 2.2b	4.0 ± 1.6b

^aResults are from all tests of females 6 to 19 days postemergence ($n = 56$). CB, color break.

^bMaximum fly density is defined as the maximum number of flies on the sphere at any given time during the 30-min assay.

^cModal fly density is defined as the mean number of flies which were most frequently seen on the sphere during the 30-min assay.

^dTotal fly seconds is defined as the total cumulative on sphere time (s) from all fly landings on a sphere during the 30-min assay.

*Mean values having the same letter within a row are not significantly different as determined by Duncan's (1951) multiple-range test.

spheres emanating the mature green papaya odor. Both maximum fly density and modal fly density increased with increasing fruit ripeness (Table III).

The order of preference for the three papaya ripeness classes for all observed behaviors was the same for females tested in the morning compared to the afternoon; however, mean response values for each of the behaviors were significantly higher in tests conducted in the afternoon (data not shown). Activity of females was greatest in age classes of 8–10 and 16 days old for most of the behaviors (Fig. 1). Eight-day-old females preferred ripe papaya odor as indicated by total fly landings, total time on sphere, maximum, and modal density, and total eggs laid. Behavior of the younger flies (6 days old) and older flies (> 10 days old) to the different odors was not significantly different. Activity in general appeared to decline with age, although 15- to 16-day-old flies appeared again to become more active.

In the field, oriental fruit flies were observed mostly on riper papayas compared to greener papayas. All of the trees had more green fruit than ripe fruit (fruit mature and ripen on the tree column at the same time, thus most fruit classes can be found on the tree, although greener fruit are in greater abundance on the tree column); however, more flies could be found on the riper fruit than on the greener fruit (Fig. 2). Of the three ripeness classes tested in the flight tunnel (mature green, color-break-one-fourth ripe, and full ripe), ripe fruit harbored more flies in the field.

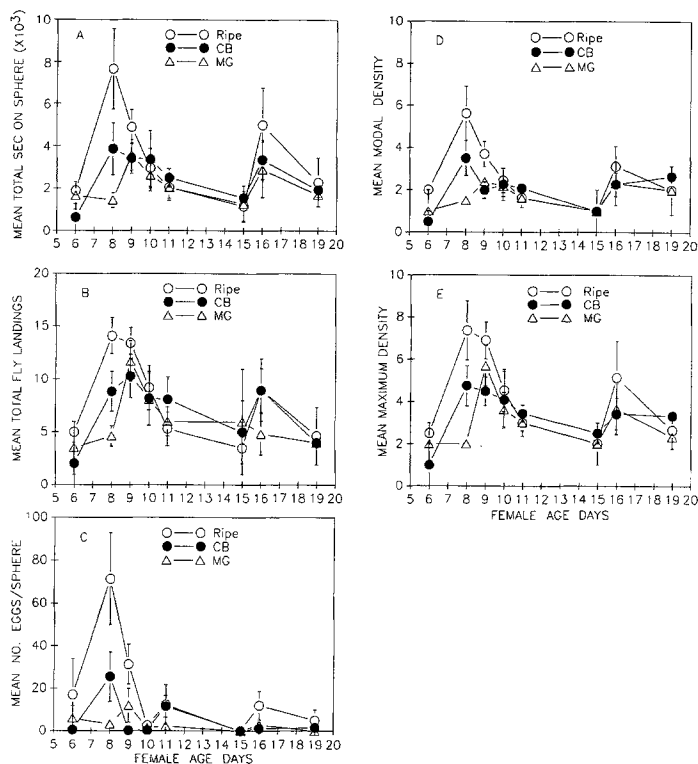


Fig. 1. Behavioral responses of female oriental fruit flies of different ages to yellow polyethylene spheres emitting odor from fully ripe, color-break to one-fourth, or mature green papayas in a laboratory flight tunnel. (A) Mean total time of all flies on the sphere during the 30-min assay. (B) Mean total cumulative fly landings from all flies visiting the sphere during the 30-min assay. (C) Mean total number of eggs laid in the sphere by all flies during the 30-min assay. (D) Mean modal density of flies on the sphere (number of flies most often noted on the sphere) during the 30-min assay (E) Mean maximum density of flies observed on the sphere during the 30-min assay. Values represent the means \pm SE of at least four tests of each age grouping. For all behaviors, the responses to the three different odors were significantly different from each other for day 8 tests ($P < 0.05$).

DISCUSSION

Female oriental fruit flies are able to use olfactory cues to discriminate among green and ripe papaya fruit in the laboratory and presumably in the field. Although females have been known to infest fruit of all different ripeness classes (Kleck, 1949; Liquido *et al.*, 1989), it is primarily the ripe fruit that are most likely to be infested in the field (Seo *et al.*, 1982; Couey *et al.*, 1984; Liquido and Cunningham, 1990). Proportionally more flies can be found in the field on

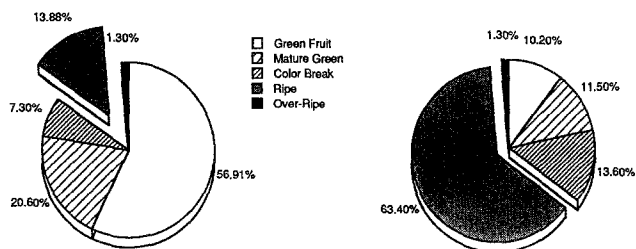


Fig. 2. Left: Pie chart of the percentage distribution of papaya fruit of different maturity classes on 30 randomly selected trees in an unharvested papaya field near Hilo, Hawaii. Mean numbers of fruit per tree \pm SE are as follows: green fruit, 13.40 ± 0.97 ; mature green, 3.67 ± 0.46 ; color-break, 1.30 ± 0.26 ; ripe, 2.47 ± 0.37 ; overripe, 0.23 ± 0.12 . Right: Percentage distribution of wild oriental fruit flies on papaya fruits of different ripeness classes from the same 30 trees. Mean numbers of flies per tree \pm SE are as follows: green fruit, 0.80 ± 0.23 ; mature green, 0.90 ± 0.26 ; color-break, 1.07 ± 0.27 ; ripe, 4.97 ± 0.86 ; overripe, 0.10 ± 0.07 .

riper fruit even though there is a greater abundance of green fruit on the tree at a given time (Fig. 2). This suggests an increase in attractiveness, arrestment, or ovipositional behaviors on the ripe fruit, which correlates with our laboratory results. Flath *et al.* (1990) reported that as intact papayas ripen, there is a change in the chemical composition of organic volatile constituents which is most apparent in the fully ripe fruit. Numerous esters and monoterpenes were found only in the headspace of ripe papayas, while substantial increases in the amount of linalool, linalool oxides, BITC, and phenylacetonitrile over those in greener fruit were also noted. Seo *et al.* (1983) found that when increasing amounts of BITC were added to guava puree, female oriental fruit flies laid fewer eggs as the concentration of BITC in the air increased from 1.9 to 8.4×10^{-10} mol/liter. However, in a similar experiment using ripe papaya puree, they found that a 10-fold increase in volatile BITC in the air was needed to reduce oviposition. BITC levels near uninjured green fruits in a papaya orchard (1.8 to 3.9×10^{-12} mol/liter of air) were not high enough to deter oviposition. They suggested that high levels of BITC in tissue of green fruit, especially those which had been punctured by ovipositing females, may deter females from ovipositing in the greener fruit. Furthermore, they noted that possibly volatile compounds produced by ripe papayas may be attractive to females and that these compounds may mask or counteract the deterrent effect of BITC. Our results suggest that perhaps it is the increase in odors characteristic of ripe fruit (esters, monoterpenes) rather than the presence or absence of BITC which females utilize to assess initial papaya suitability. The increased levels of BITC reported by Flath *et al.* (1991) in ripe papayas were apparently not high enough to deter females from ovipositing. The level of BITC in papaya tissue (which decrease with

ripening) may still, however, be important in gustation by sensory receptors on the female's ovipositor.

These findings and the present results showing a significant preference of females for ripe papaya odor using several behavioral parameters suggest that odors characteristic of ripening fruit such as esters or monoterpenes may be important to the females in assessing olfactory suitability. Esters from ripe apple varieties have been found to be key olfactory stimuli for the apple maggot, *Ragoletis pomonella* (Fein *et al.*, 1982; Ressig *et al.*, 1982; Carle *et al.*, 1987; Averill *et al.*, 1989). Many esters and oxygenated monoterpenoids (i.e., linalool and linalool oxides) also elicit some of the highest electroantennogram responses in oriental fruit flies (Light and Jang, 1987, unpublished) as well as being attractive synergist to fruit odors of other tephritid species (Light and Jang, 1988; E.B.J. and D.M.L., unpublished). Our results prove that females utilize olfaction to assess the attractiveness of a fruit and, perhaps, along with other sensory inputs such as vision, gustation, and tactile stimuli, the fruit's suitability for eventual oviposition and larval host utilization. Oriental fruit fly females exhibit several different behaviors in order to assess substrate suitability for oviposition including antennal and tarsal palpations, proboscis extension, and ovipositor dragging and probing. Although the color and shape of spheres used in these tests were standardized, any potential problems with the fly's integration of vision with olfactory sensory inputs (i.e., green papaya odor from yellow sphere) were apparently overcome by the female's ability for olfactory discrimination. Perhaps discriminatory behaviors would be further enhanced by pairing odor with appropriate shape and color. Our studies support in part the hypotheses of Liquido *et al.* (1989), who suggested that female ovipositional preference rather than egg and larval survivorship may be the key to differential infestation of papayas by oriental fruit flies.

Oriental fruit flies can be found active in and around papaya fruit throughout the day but are known to mate primarily in the late-afternoon to dusk period (Kobayashi *et al.*, 1978). We found no difference in overall ranking of the preferred papaya odors in our laboratory behavioral bioassays of females tested in the morning versus the afternoon. However, mean responses for most of the noted behaviors were actually higher for afternoon tests than in morning tests of our laboratory-reared flies. Wild females were not tested and may differ from their laboratory-reared counterparts. We did notice a significant trend in responses with female age for all of the observed behaviors. The laboratory-reared females appeared to show a significantly greater response at 8–10 days after emergence, resulting in a preference for the ripe papayas over the two other ripeness classes (Fig. 1). This response level then declined, but activity increased again at 15–16 days postemergence. Age-specific responses of apple maggot flies to synthetic apple volatiles have also been reported (Averill *et al.*, 1989).

Field observations of oriental fruit fly distribution on papayas confirm our laboratory results and several previous field studies. Thus the preference of oriental fruit fly females for the odor of riper fruit might appear to maximize the potential of larval survival by avoiding greener fruit, which are potentially high in toxic allelochemicals such as benzylisothiocyanates in the fruit tissues. Ripe fruit odor may also represent other nutritional advantages such as an increase in free sugars. Future work on identifying specific semiochemicals which influence attractancy, deterrence, or oviposition may provide additional clues helpful in developing control strategies against this insect.

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